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Suitability and Selection of Territorial Sites Used by Male Blue Grouse

by

Richard Arnold Lewis

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A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF Master of Science

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1979

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled Suitability and Selection of Territorial Sites Used by Male Blue Grouse submitted by Richard Arnold Lewis in partial fulfilment of the requirements for the degree of Master of Science.

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Abstract

Pattern of occupancy of territorial sites used by male blue grouse (Dendragapus obscurus fuliginosus) was examined on a 485 ha area (Comox Burn) on Vancouver Island, British Columbia. Numbers of territorial males increased from 1969 to 1971, then remained relatively stable at approximately 80 males per year to and including 1978. Some sites were used for territories every year while others showed intermittent use. Sites used at least 9 of 10 years were termed "persistent", those used less than 9 years "transient". Over a period of 10 years (1969-1978) there were 41 persistent and 82 transient sites on Comox Burn.

Males occupying persistent sites survived longer and more females were found near their territories in early spring than those on transient sites. Thus, males using persistent sites may be more successful, reproductively, than those using transient sites. Experimental removal of males from persistent and transient sites indicated that males preferred persistent sites for territories.

Although males occupying the two types of sites had different rates of survival, no vegetative or topographic differences were found between persistent and transient sites. Vegetative parameters measured included availability of food and cover and evaluations of "openness". Slopes around activity centres and height of territories in relation to surrounding areas were the topographic features investigated. The alternative, that demographic differences

between males utilizing the two types of site are due to behavioural differences between the two groups of males is considered unlikely. Physical differences between persistent and transient sites may be subtle, rather than marked, and more intensive examinations may be required.

My results have several immediate and evolutionary implications. Support for the hypothesis that yearling males are nonterritorial, hence non-breeders, because it is advantageous for them to delay breeding is presented. Also, evidence from the removal experiment suggests that "surplus" non-breeding adult males were present on Comox Burn. Therefore, the role of adult males and territorial behaviour in regulating breeding density in populations of blue grouse is reexamined. These results are discussed in relation to present knowledge of population regulation in blue grouse and general theory on population ecology.

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Introduction

Research on populations of blue grouse (Dendragapus obscurus fuliginosus) on Vancouver Island, British Columbia over the past 25 years has been aimed at determining how breeding densities are regulated (Bendell and Elliott 1967; Bendell et al. 1972; Zwickel 1972; Zwickel and Bendell 1967, 1972; Zwickel et al. 1979). Male blue grouse are promiscuous (Bendell and Elliott 1967; Wiley 1974) and they establish territories from which they attempt to attract females by hooting (singing) (Bendell and Elliott 1967; McNicholl 1978). Although possession of a territory is generally regarded as a prerequisite for breeding and most yearling males are not territorial, territorial behaviour has not been considered important in limiting breeding densities (Bendell and Elliott 1967). A major reason for this conclusion was that even in dense populations all available space was not occupied by territorial males (Bendell and Elliott 1967). However, presence of unused areas makes non-breeding by yearling males puzzling since they are physiologically able to breed (Simard 1964). Some territorial sites are occupied continuously and others only intermittently (Bendell and Elliott 1966, 1967). Therefore, some areas that are unused each year are apparently suitable for territories. Why do yearling males not occupy these vacant sites? Also, how does the pattern of territorial occupancy (i.e. continuous and intermittent) displayed by males relate to our present knowledge of population

regulation in blue grouse? My objectives were to seek answers to these questions. I examined use of territorial sites by males on one area over a 10 year period and related the pattern of use to the suitability of these sites for territories. Results are presented in the form of 3 papers:

1. Patterns of occupancy of territorial sites by male blue grouse.
2. Removal and replacement of male blue grouse on a series of persistent and transient territorial sites.
3. Characteristics of persistent and transient territorial sites of blue grouse.

The pattern of use of territorial sites by males on one area over a 10 year period (1969-1978) and the reproductive potential of males occupying different sites are considered in the first paper. Following this study a removal experiment was undertaken to compare rates of replacement between sites used persistently and those occupied intermittently and these results are presented in the second paper. Vegetative and topographic characteristics of territorial sites are examined in the third paper. Differences between sites used continuously and intermittently are sought.

A final discussion briefly describes general theories on population regulation and relates research on blue grouse to them. My studies are then considered in relation to previous studies and theory.

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Paper 1: PATTERNS OF OCCUPANCY OF TERRITORIAL SITES BY MALE BLUE GROUSE

Abstract

Pattern of use of territories by male blue grouse (*Dendragapus obscurus fuliginosus*) was examined on a 485 ha area, over a 10 year period (1969-1978), on Vancouver Island, British Columbia. Some sites were used for territories every year, usually by a succession of males; others were used only sporadically. These have been called "persistent" and "transient" sites, respectively. Males using persistent sites survived significantly longer than those occupying transient sites. In early spring more females were found near persistent than transient sites. Thus, males occupying persistent sites apparently have greater reproductive potential than those utilizing transient sites. Activity centres of territories tended to be uniformly distributed and there was no evidence of transient sites being clustered around persistent sites. This pattern of territorial occupancy has both immediate and evolutionary implications.

Introduction

Gullion (1967) and Boag (1976) noted that some sites used for territories by male ruffed grouse (Bonasa umbellus) were occupied every year while others were used only intermittently. A similar pattern of occupancy was observed for blue grouse (Bendell and Elliott 1966). However, data from only four years were used to make this observation and this is an insufficient amount of time to fully evaluate patterns of territorial use. Blue grouse have now been studied for 10 consecutive years (1969-1978) on an area near Courtenay, Vancouver Island, and these data allow a closer examination of the use of territorial sites over time by male blue grouse.

Boag (1976) suggested that frequency of occupancy reflects the suitability of sites for territories. In blue grouse, occupancy of a territory permits males to display to and mate with females without interference from other males (Bendell and Elliott 1967). Since male blue grouse are promiscuous (Bendell and Elliott 1967; Wiley 1974a), they can increase breeding success by living a long time and/or by mating with several females in any one year. Sites with characteristics that enable males to maximize breeding success would be considered optimal and should be selected for territories.

The purpose of this study was to examine the pattern of occupancy, over time, of territorial sites used by male blue grouse. Differences in survival and breeding potential of

males occupying different sites were also investigated. Relationships between the observed pattern of use and population parameters, such as recruitment of males into breeding populations, are discussed.

Territory is defined as the area used, and presumably defended, by individual males for displaying to and breeding with females (Bendell and Elliott 1967). The area within the territory where the resident most frequently hoots (sings) is termed the activity centre. Territorial sites are the specific locations on the study area where territories are found. Although territorial boundaries on a given site may change slightly from year to year, the location of the activity centre generally remains the same.

Study Area

This study was conducted by using data collected between 1969 and 1978 on Comox Burn, a 485 ha area on the east slope of Vancouver Island, approximately 14 km west of Courtenay. This area is in a region intermediate between the Douglas fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla) biogeoclimatic zones (Krajina 1965).

Between 1947 and 1961, Comox Burn was clearcut and in September, 1961 the entire area was burned by wildfire. Replanting with Douglas fir was almost complete by 1964. In 1969 vegetative structure consisted entirely of "open" (Bendell and Elliott 1967) and "very open" types. By 1977 portions had become "dense" or "very dense", but the majority of the area was still "open" (Figure 1). For a more detailed description of the study area see Zwickel and Bendell (1967, 1972).

Methods

Populations of blue grouse were studied from April to late August or early September each year. Grouse were found with the aid of pointing dogs and locations of all birds sighted were recorded. Attempts were made to capture and color-band all unmarked birds. Throughout the study, roughly 80% of the territorial males were banded. In spring, males on territories hoot frequently and this aided in their detection and identification. By mid-May each year most territorial males had been located and individually identified, if banded.

Locations of all banded territorial males and unbanded and unidentified males found hooting were plotted for each year on maps of the study area. All singing males were considered to be on territories, since hooting is used by males to signify occupancy of a territory (Bendell and Elliott 1967; McNicholl 1978). Only one sighting of a hooting male was used, in a few cases, to consider a territorial site occupied in a given year.

All statistical comparisons were made with t-tests or chi-square tests unless otherwise noted. A probability level of 0.05 or less was considered significant.

Results

As with ruffed grouse (Gullion 1967; Boag 1976), some sites were used for territories every year, others only intermittently (Table 1). Those used every year generally had a succession of males occupying them as only one male present in 1969 was still alive in 1978. A site was termed "persistent" (equivalent to perennial centres of Boag (1976) and Gullion (1967)) if it was occupied for at least nine of the ten years. Areas used nine years were considered persistent since non-use in one year may have been due to chance. Sites used eight years or less have been called "transient". Thirty-eight transient sites had periods of use separated by intervals when they were vacant. From 1969 to 1978 there were 41 persistent and 82 transient sites on Comox Burn. During this time numbers of territorial males varied from 68 to 85. In some years individual males occupied areas normally used by two different males, but this was uncommon (12 instances). The number of transient sites used each year ranged from 31 to 44 (Table 2).

Males that had occupied a territory in one spring but were not sighted in subsequent years were assumed to have died. This seems a valid assumption since males seldom shifted territories from one year to the next and any shifts were generally to adjacent territories (Lewis 1979). The average survival of males occupying the two types of sites was used as one measure of the quality of those sites. Only banded males were used to estimate survival. Estimated

survival on the two types of site (Table 3) is minimal because males occupying territories at the end of the study (1978) were included in survival estimates and classed as not living beyond 1978 even though most would not die before 1979. Males occupying territories at the beginning of the study (1969) were also used in estimating survival but since some banding operations had been conducted on Comox Burn between 1962 and 1969 the effect of these males on minimizing survival is slight. The year of banding was considered the first year of territorial occupancy for these individuals. As a result of including these males one individual was recorded as living 11 years even though the period of study was only ten (Table 3). Newly banded males occupying sites that had an unbanded occupant in the previous year were not included in these calculations, nor were males that shifted territories during the study. Survival would have been further underestimated if these males had been included. Males using persistent sites survived significantly longer than those using transient sites (Mann-Whitney U-test, $U = 5304.5$, $p < 0.001$) (Table 3).

Sites may have been occupied persistently merely because males on these areas survived a relatively long time (Table 3). To examine this possibility, I compared numbers of males using persistent sites to those using transient sites. Newly banded males were considered new individuals even if the site they used had been occupied by an unbanded

male in the previous year. If a site was occupied by an unbanded male for a succession of years, this was considered as one male. These criteria result in the number of males occupying sites being overestimated, but I assume that the overestimation is roughly similar for both groups. Average number of males per persistent site (3.20) was greater than for transient sites (2.16). Thus, even though males using persistent sites survived longer, these sites had a greater turnover of males than transient sites. Consequently, it seems unlikely that persistent sites were classified as such simply because individuals occupying these areas survived longer than those using transient sites.

As noted above, males can increase their fitness by mating with more than one female each year. Copulations, however, are rarely observed in the field and it is difficult to determine if some males are breeding more than others. Thus, indirect evidence was used to examine this possibility.

Locations of all females sighted prior to 16 May were plotted for each year to test the hypothesis that males on persistent sites attract, and potentially mate with more females than those occupying transient sites. Locations prior to 16 May were used because most breeding on Comox Burn is completed by this time (Zwickel 1977). For each location I determined whether the hen was nearer the activity centre of an occupied persistent or transient site. More females were found near persistent (444) than transient

sites (301). These data differed significantly from a ratio of 399:371 (Table 2), the expected ratio if males on transient sites attract females equally as well as those on persistent sites ($p < 0.001$).

Even though more females were found near persistent than transient sites this may not be because males on persistent sites attract more females. Persistent sites may simply represent habitat that is preferred by females. On arrival on breeding ranges in spring the primary requirement of females is likely to secure a nesting area (S. J. Hannon, pers. comm.). If habitat around persistent sites is most suitable for females, more nests should be found here than around transient sites. Between 1969 and 1978, 113 nests were found on Comox Burm. Thirty-nine were nearer activity centres of persistent sites, 74 nearer activity centres of transient sites. This does not differ significantly from the expected ratio of 1:2 (41 persistent sites, 82 transient sites) if habitat near transient sites is as good for nesting as that near persistent sites ($p > 0.05$). Thus, males on persistent sites may be attracting more females than those on transient sites. That males are attracting females during spring is further suggested by the fact that significantly more females were found near transient sites when they were occupied than when they were unoccupied (301 vs. 107, respectively, compared to an expected ratio of 371:449) ($p < 0.001$). Field workers in spring, however, may spend more time searching areas where territorial males are

located than where no males are present. This would affect this result but the bias is likely negligible.

Weights of males occupying persistent and transient sites were compared to see if body size might be a factor in determining which type of site was obtained. Average weights of newly banded males, most of which are assumed to be two years of age, that obtained persistent sites (1287 ± 16g, N = 17) did not differ significantly from those of newly banded males on transient sites (1293 ± 13g, N = 39) ($p > 0.05$). Median date of capture was roughly similar for both groups (17 May vs. 12 May, respectively). When weights of males banded as yearlings which subsequently returned as adults were compared, those that obtained persistent sites weighed less (1102 ± 23g, N = 12), on average, as yearlings than those that acquired transient sites (1164 ± 15g, N = 24) ($p < 0.05$).

Gullion (1967, 1976) and Boag (1976) both noted that activity centres of ruffed grouse tended to occur in groups or clusters, although each postulated different reasons for this phenomenon (structure of habitat and social interaction, respectively). A similar occurrence in blue grouse seems possible since McNicholl (1978) demonstrated that males tend to sing in groups. To test this idea, I measured the distance from the activity centre of each territory to the activity centre of the nearest adjacent territory. All territorial sites were used in this measurement even if they were not occupied in every year. I

then calculated an R value (Clark and Evans 1954) which gives a measure of the dispersion of activity centres on Comox Burn. R values can range from 0, indicating maximum clumping, to 2.1491, representing uniform spacing. A value of 1 signifies that activity centres are randomly distributed. The estimated R value was 1.3346 indicating a significant tendency for activity centres on Comox Burn to be uniformly spaced (see Figure 1) ($c = 4.68$, $p < 0.01$, Clark and Evans 1954).

Boag (1976) further suggested that transient centres were grouped around perennial centres. Although activity centres on Comox Burn tend to be uniformly distributed, transient sites may be located principally around persistent sites, as opposed to a distribution in which persistent and transient sites are randomly dispersed in a uniform pattern. I therefore plotted 82 random points on the study area and determined whether the activity centre of a transient site or a random point was nearer the activity centre of a persistent site. If transient sites are randomly spaced in relation to persistent sites an equal number of transient sites and random points should be found nearer to persistent sites. This was the case (18 vs. 23, respectively, $p > 0.05$). Thus, transient sites were not located preferentially around persistent sites.

Discussion

Males occupying persistent sites survived longer and had more females found near their territories than those using transient sites. Thus, as Boag (1976) suggests, persistent sites are apparently more suitable than transient sites for territories. Since the number of persistent sites on Comox Burn is limited, there may be intense competition among males for these areas. What determines which males obtain persistent sites? Males securing persistent sites did not weigh more, either as yearlings or adults, than males procuring transient sites. Body weight therefore, does not appear to be important in determining which type of site is obtained. Weights of individuals captured from April to September were used for this analysis while competition for territories occurs in March and early April. It is unlikely however, that this would affect the results since male blue grouse do not undergo significant weight changes from April to September (Redfield 1973). Lance (1978) suggested that body condition of red grouse (Lagopus lagopus scoticus) was important in determining where males settled as adults.

Male blue grouse usually do not hold territories as yearlings (Bendell and Elliott 1967; this study), but tend to localize their movements in an area encompassing the territories of several males (Sopuck 1978). Yearlings may evaluate the suitability of these sites for territories at this time, for as young adults most males return to the same areas they occupied as yearlings (Sopuck 1978). When two

year old males arrive on breeding ranges in spring, following migration, some territorial sites will be vacant because of adult mortality during the preceding year. These new adults should attempt to secure the best territorial sites available and once a site is secured it is unlikely to be lost to an intruder (McNicholl 1978). Whether or not a two-year old acquires a persistent site will depend, in part, on how many persistent sites became vacant in the area he occupied as a yearling. It may also depend on being the first to find and recognize that a site is not occupied. Chance, therefore, is likely one factor determining whether or not a particular male obtains a persistent or transient site.

Over the ten year period of this study vegetative structure on Comox Burn changed dramatically. In 1969 Douglas fir plantations were still at early stages of regeneration. By the final two years of the study some areas were entering "very dense" stages (Figure 1). Because recruitment to populations of blue grouse is not affected by density of conifers until "very dense" stages are reached (Redfield et al. 1970), I believe that the changes in vegetative structure from 1969 to 1978 likely had little effect on the status of a site in terms of its suitability as a territory. There was no evidence that transient sites were found more often in areas where vegetative structure had changed the most during this time (Figure 1). This contrasts to Boag's (1976) report for ruffed grouse where

changes in vegetative structure around perennial centres, occurring over short periods of time, resulted in some becoming transient.

A general absence of territorial behaviour in yearling males seems important because they are physiologically capable of breeding (Simard 1964). Also, approximately half of the transient sites were vacant each year. Thus, some yearlings must delay breeding. Wiley (1974a, b) postulates several reasons for the evolution of delayed breeding. If early survival and later reproduction are enhanced by delaying breeding, such a system could evolve (Wiley 1974b). Yearling males likely could not compete with adult males for persistent sites and taking transient sites would result in life expectancy being reduced. The advantage in possessing a persistent site would be even greater if males on these sites are performing most of the breeding, as is the case with dominant males in several lek-forming species (Ballard and Robel 1974; Kruijt et al. 1972; Wiley 1973, 1974a). This seems possible since more females are found around persistent than transient sites in early spring. Therefore, it may be advantageous for yearling males not to select transient sites, but instead to delay breeding until becoming adult when chances of obtaining a persistent site are presumably increased. Nevertheless, life expectancy declines with age. Thus, it may not be advantageous for adult males to delay breeding, so some individuals not securing persistent sites would settle on transient sites

and attempt to breed on them.

The pattern of use of territorial sites displayed by male blue grouse suggests that territorial behaviour should not be limiting numbers of adult males obtaining territories. Bendell and Elliott (1967) also concluded that territorial behaviour was not determining numbers of blue grouse. A "surplus" of adult males should not exist since many transient sites are vacant each year. Indeed, several past removal studies failed to detect a surplus of adult males among populations of blue grouse ((Bendell and Elliott 1967; Bendell et al. 1972; Zwickel 1972). However, Lewis (1979) provides evidence which suggests that surplus adult males are present in blue grouse. Regardless of whether or not there are surplus adult males, how should yearling males be considered? They are physiologically able to breed but apparently do not do so. Between 1969 and 1978, 141 banded yearlings were identified on Comox Burn and only one was territorial. Potential breeders, that do not breed, are therefore present in populations of blue grouse. Removal experiments have demonstrated that yearling males will occupy territories if adult males are not present (Bendell et al. 1972; Zwickel 1972). Presence of potential breeders that are prevented from doing so by residents, is one requirement that must be satisfied if territorial behaviour is to limit numbers of breeders (Klomp 1972). A second requirement, that all suitable space for territories be occupied (Klomp 1972), is apparently not true in blue

grouse. However, if yearling males delay breeding to increase their chances of obtaining a persistent site, optimal areas (e.g. persistent sites) may be the only space which should be considered. Since territorial behaviour seems to limit numbers of males occupying optimal areas, and hence may be a factor causing yearling males to delay breeding, it should not be ruled out as a factor determining numbers of breeding males.

Following a slight increase in numbers of territorial males on Comox Burn from 1969 to 1971, numbers remained relatively stable at approximately 80 males. This occurred despite large fluctuations in annual production (Zwickel et al. 1979). If transient sites correspond to the Level 2 or suboptimal habitat of Brown (1969), numbers of males occupying transient sites should fluctuate in relation to annual production. Why has this not occurred (Table 2)? Perhaps yearlings are interacting among themselves and some exclude others from an area. This would increase the chance of those not excluded obtaining a persistent site. Interaction among yearlings is suggested by the fact that surplus yearlings are available for recruitment to areas where residents have been removed (Bendell et al. 1972; Zwickel 1972). Alternatively, Zwickel (1972) hypothesizes that adults may be excluding yearlings. As a result of these interactions numbers of yearling males on an area may remain relatively stable from year to year. Since annual mortality is also relatively constant (Zwickel and Bendell 1967), this

could account for the stability in numbers of adults using transient sites each year.

In conclusion, territorial sites used by male blue grouse differ in their suitability as breeding sites. These differences result in some sites being used every year, others only sporadically. This pattern of use has several immediate and evolutionary consequences. Two important questions remain to be answered. First, how do persistent and transient sites differ, and how do these differences affect a territory's suitability as a breeding site?

Acknowledgments

I wish to extend sincere thanks to F. C. Zwickel for his helpful guidance and unlimited discussion. W. G. Evans, J. O. Murie, and fellow graduate students, S. J. Hannon and L. G. Sopuck also provided useful comments and suggestions. Several graduate students and undergraduate summer assistants collected field data. Their contribution is greatly appreciated. Field studies were conducted on lands of Crown Zellerbach of Canada Limited and financial support was provided by the British Columbia Fish and Wildlife Branch, the National Research Council of Canada, and the University of Alberta.

Table 1: Frequency of use of territorial sites occupied by male blue grouse on Comox Burn, 1969-1978.

Number of years used	1	2	3	4	5	6	7	8	9	10
Number of sites	7	12	9	12	13	11	11	7	11	30

Table 2: Number of persistent and transient territorial sites occupied by male blue grouse on Comox Burn, 1969-1978.

Year	Territorial Sites Occupied		
	Persistent	Transient	Total
1969	37	32	69
1970	39	31	70
1971	40	42	82
1972	41	41	82
1973	41	42	83
1974	41	37	78
1975	41	32	73
1976	38	34	72
1977	41	44	85
1978	40	36	76
Total	399	371	770

Table 3: Survival of male blue grouse occupying persistent and transient territorial sites on Comox Burn, 1969-1978.

	Survival (yrs)												
	1	2	3	4	5	6	7	8	9	10	11	Mean	N
No. of males from persistent sites	12	11	15	10	11	8	6	3	1	3	1	4.25	81
No. of males from transient sites	34	21	15	10	6	5	2	1	0	0	0	2.60	94

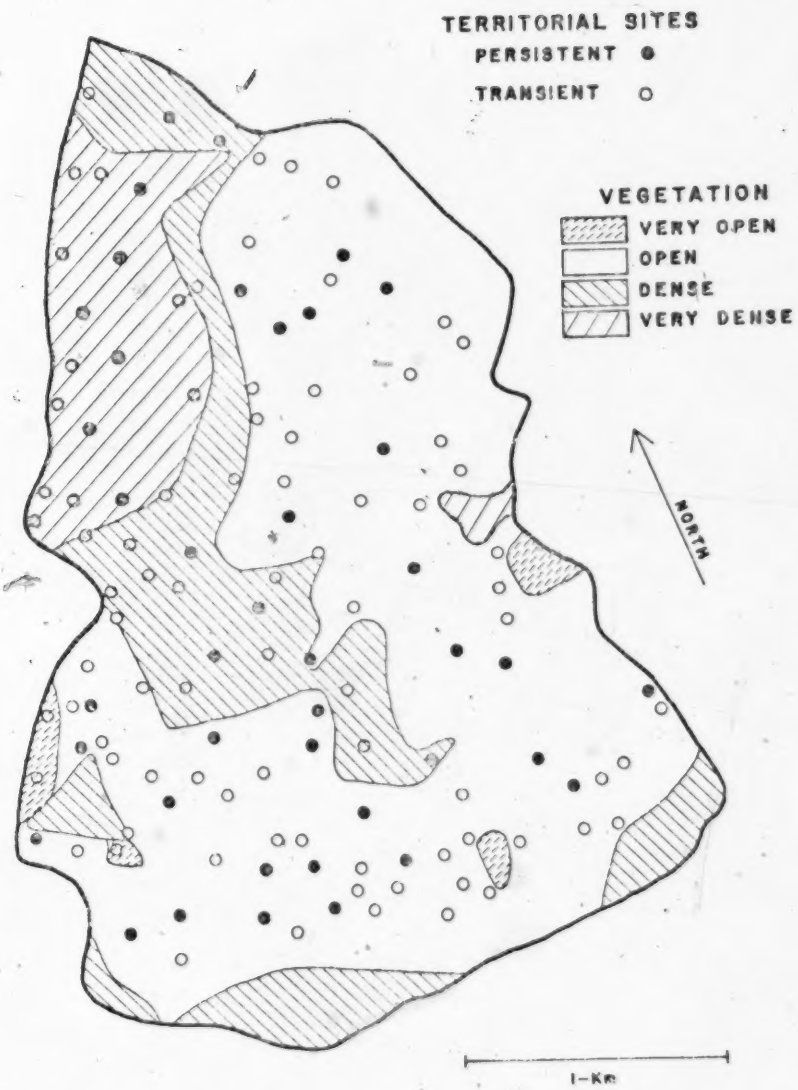

Figure 1: Vegetative structure (after Bendell and Elliott 1967) in 1977 and dispersion of activity centres of persistent and transient sites on Comox Burn.

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Paper 2: REMOVAL AND REPLACEMENT OF MALE BLUE GROUSE ON PERSISTENT AND TRANSIENT TERRITORIAL SITES

Abstract

Original occupants and subsequent replacements were removed from a series of "persistent" and "transient" territorial sites (Lewis 1979) of blue grouse (Dendragapus obscurus fuliginosus). Significantly more replacement males settled on persistent sites. Most replacement males were adults which likely would have remained nonterritorial, hence been non-breeders, if persistent sites had not been made available through artificial removal. Replacement males had smaller testes than those of resident males collected at comparable times. Existence of nonterritorial adult males suggests that territorial behaviour may limit breeding densities of adult males in populations of blue grouse. This possibility, and other implications raised by this experiment are discussed.

Introduction

Some sites used by male blue grouse for territories are used every year ("persistent" sites) while others are occupied only intermittently ("transient" sites) (Lewis 1979). Approximately half of the transient sites on one study area were vacant each year. Males on persistent sites survived longer and had more females found near their territories than males occupying transient sites. These results suggest that persistent sites are better than transient sites for satisfying the display and mating functions of territories of blue grouse (Lewis 1979). If persistent sites are most suitable, males should preferentially select these areas for territories.

Possession of a territory is generally considered a prerequisite for breeding (Bendell and Elliott 1967). I also used my results noted above to suggest an explanation for the near absence of territorial behaviour among yearling male blue grouse (Bendell and Elliott 1967). I hypothesized that yearling males, which are physiologically capable of breeding (Simard 1964), could not compete with adults for persistent sites, and rather than select transient sites for territories they delayed breeding until adulthood, when chances of obtaining a persistent site might be greater. The general phenomenon of delayed breeding has been discussed in more detail by Selander (1965) and Wiley (1974a, b). If my argument is true, yearlings should take territories if persistent sites are available. Indeed, past removal studies

with blue grouse have demonstrated that yearlings will occupy territories when adults are removed (Bendell and Elliott 1967; Bendell et al. 1972; Zwickel 1972). However, in those studies quality of sites was not determined and it was impossible to tell if yearlings that took territories selected only optimal sites.

The objective of this study was to test the hypothesis that males prefer persistent sites for territories. This was done by undertaking an experiment in which original occupants and all subsequent replacements were removed from a series of persistent and transient sites. If the hypothesis is correct, replacement males should preferentially settle on persistent sites. Since persistent sites were made available artificially it also served as a test for the hypothesis that yearling males delay breeding because they are unable to obtain persistent sites. This experiment was carried out in the spring of 1978.

Study Area

The area used for this experiment was basically that of Lewis (1979) and territorial sites had already been classified as persistent or transient. This 485 ha area, Comox Burn, lies on the east slope of Vancouver Island approximately 14 km west of the town of Courtenay, in a region intermediate between the Douglas fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla) biogeoclimatic zones (Krajina 1965). The area was clearcut between 1947 and 1961, and in September 1961 was burned by wildfire. Replanting with Douglas fir was essentially complete by 1964. In 1977 vegetative structure of most of the area was "open" (Bendell and Elliott 1967), but some areas were becoming "very dense" (Figure 1). Since replacement to populations of blue grouse begins to decline as "very dense" stages of vegetative structure are approached (Redfield et al. 1970) all removal sites were selected in areas classified as "open" in 1977 (Figure 1). More details concerning Comox Burn can be found in Zwickel and Bendell (1967, 1972).

Methods

Locations of territorial males on Comox Burn were determined in early April. Pointing dogs and hooting (singing) by these males aided in their detection. Most males occupying territories had been located and individually identified, if banded, by 11 April. Removal, by shooting, of original occupants of persistent and transient sites began at this time. Although some transient sites are vacant each year, only areas occupied in 1978 were used in this experiment to ensure that all experimental transient sites were acceptable as territories in 1978. Males were removed as quickly as possible and the number of persistent and transient sites vacant was about equal at any given time (Table 1). This reduced any potential bias that would be produced by having a greater number of one type of site vacant at any one time. Original occupants of 11 persistent and 11 transient sites had been removed by 25 April. Removal of original occupants was terminated at this time leaving several territories in adjacent areas still occupied. Efforts were then concentrated on removal of replacement males.

Experimental sites were generally searched on a daily basis, usually by two people. An attempt was made to check each of these sites at least once a day and on most days some sites were checked twice. Any males that settled on removal sites were shot. Mere presence of a male was not sufficient as a criterion for replacement. Males were considered to have settled only if they were seen hooting.

This implies that the male is using and defending the area since hooting is used by male blue grouse to announce occupancy of a territory (Bendell and Elliott 1967; McNicholl 1978). Further, males had to be hooting within the activity centre (Lewis 1979) of a removal site. This criterion was added to ensure that adjacent males had not merely expanded their territories onto the edge of vacated sites after previous residents had been removed. Most replacement males were removed within a day after settling on a vacated site.

Necropsies were performed on all collected birds. Testes and spleens were weighed on a portable single beam balance accurate to 0.01g, other body organs on a triple beam balance accurate to 0.1g (some organs were destroyed by shot and were unavailable for analysis).

T-tests or chi-square tests were used for all statistical comparisons and probability levels of 0.05 or less were considered significant.

Results

Evidence that males prefer persistent sites for territories initially came from an examination of territorial shifts made by individual males on Comox Burn between 1969 and 1978. During this period, 11 males moved from transient to persistent sites while only 3 made the reverse move. These data are significantly different when compared with an expected ratio of 1:2 (on Comox Burn there were twice as many transient as persistent sites) ($p < 0.001$).

The first replacement male was removed on 13 April. Males continued to settle on removal sites until 1 June, with 1 to 5 replacements removed per week (Figure 2). Median time for recruitment, following removal of prior occupants, was 10 days, although 2 replacements occurred as soon as 2 days after an occupant had been removed.

Significantly more replacement males settled on persistent than transient sites (20 vs. 4, respectively) ($p < 0.01$). Seven persistent sites had more than one replacement while maximum replacement on a transient site was one (Table 2). Only 4 males (17%) shifted from neighbouring territories and all were to persistent sites. Since I attempted to remove males as soon as they were found hooting on a removal site, I do not know whether males that shifted had abandoned their former territories or whether both areas would have been used.

Only 2 yearlings settled on removal territories and both selected persistent sites. With the exception of the 4

males that shifted territories, the remainder of the replacements (18) were adults that had not previously been recorded as territorial on Comox Burn. Twelve had previously been banded as adults, yearlings, or juveniles, all on Comox Burn or an immediately adjacent area. It is unlikely that any had occupied territories off the study area since adult males tend to return to the area they occupied as yearlings (Sopuck 1978). Also, as demonstrated by the infrequent number of territorial shifts made on Comox Burn, males tend to remain on their territory once one is obtained and any shifts which are made are generally to adjacent areas. Known ages of replacement adults, other than those shifting territories, ranged from 2 to at least 5 years (Table 3).

Mean weight of new (i.e. those having no previous history of territorial occupancy) adult replacements (1240 ± 24g, N = 16) did not differ from that of a sample of banded territorial males (1284 ± 11g, N = 50) from Comox Burn between 1970 and 1978 ($p > 0.05$). Weights of only 16 replacements were used as two were not recovered after being shot. Small sample size (2) precludes any statistical comparison between weights of replacement yearlings in this experiment and yearlings that were nonterritorial. However, average weight of the 2 yearlings collected in this study (1127 ± 7.5g) did not differ greatly from that of yearlings that were nonterritorial and banded on Comox Burn between 1969 and 1978 (1107 ± 9g, N = 126). Body size therefore, did not appear to be a factor in determining whether or not

males took territories. As well, other data from necropsies (Table 4) did not reveal any differences between adult replacements and males removed as original occupants, with the possible exception of weights of testes (Figure 3).

Weights of testes of replacement adults could not be compared directly to those of original occupants because testes undergo seasonal variations in size (Simard 1964). Data on seasonal changes in weights of testes of territorial blue grouse from an area near Campbell River, Vancouver Island (40 km NW of Comox Burn) are provided by Simard (1964), however. These two areas are relatively close so it is likely that testes of blue grouse on Comox Burn undergo a similar cycle of weight change. Testes of adult replacements taking territories for the first time were distinctly smaller than those of resident males examined by Simard (1964) at comparable times while the testes of original occupants and males that shifted territories were similar in weight to those of Simard's resident males (Figure 3). However, since Simard (1964) did not provide standard errors, conclusions from these results must be viewed as tentative.

Discussion

Persistent sites received significantly more replacement males than transient sites, all shifts made by neighbouring males were to persistent sites, and both yearlings that took territories selected persistent areas. These results strongly support the hypothesis that males prefer persistent sites for territories.

Although several yearling males were known to be present on Comox Burn in 1978, only two took territories on removal sites. This does not lend strong support to the hypothesis that yearling males delay breeding because they are unable to obtain persistent sites. In previous experiments yearlings have become territorial following removal of residents (Bendell and Elliott 1967; Bendell et al. 1972; Zwickel 1972). In these cases, however, all residents were removed from experimental areas, while in my study removal sites were interspersed among occupied territories (Figure 1). The presence of established residents may have prevented yearlings from taking territories by inhibiting full sexual behaviour even though yearlings go through normal testicular cycles when adults are present (Simard 1964). Perhaps direct behavioural interactions with adult males (either established or replacement), both on and off removal sites, prevented yearlings from taking territories. If true, the hypothesis that yearling males are nonterritorial because persistent sites can not be obtained should not be rejected.

Males occupying transient sites in surrounding areas did not readily move onto vacated persistent sites despite the fact that these are preferred areas. This is not surprising as male blue grouse do not frequently change territories under nonremoval conditions. From 1969 to 1978 only 23 banded males on Comox Burn (out of 630) moved to different territories. Security is likely enhanced by site familiarity and territorial males may be reluctant to move to new areas even though they might be more suitable. Krebs (1971) found such an occurrence in great tits (Parus major). He removed territorial pairs from an area of mixed woodland (optimal habitat) and observed that most replacements were young individuals that had formerly held territories in hedgerows (suboptimal habitat). Adult birds were also occupying suboptimal habitat but did not move to the removal sites. Also, if a male moves from one territory to obtain another he may be unsuccessful and also lose the area previously held.

Adult males begin arriving on Comox Burn in late March and most occupy territories when females begin arriving in mid-April (F. C. Zwickel, pers. comm.). Even though most breeding does not occur until early May (Zwickel 1977), males may have to occupy territories when hens arrive because females may be assessing them as breeding partners at this time. However, most replacements occurred after mid-April (Figure 2). Despite the fact that many replacement males settled on territories after the time when they might

be successful in breeding in that year, by doing so, a site was secured for future years. This would be beneficial if persistent sites were obtained but since males form strong site attachments for territories, it would not be advantageous to select transient sites as chances of surviving and reproducing might be reduced (Lewis 1979).

Eighteen of 24 replacement males were adults which had no known history of territorial occupancy. Most appeared on removal sites after mid-April (Figure 2). Since established males are usually on territories at this time, it is highly probable that in the absence of artificial removal these birds would not have secured territories. Possession of a territory seems a prerequisite for breeding in male blue grouse (Bendell and Elliott 1967) and the presence of replacement adults suggests that non-breeding adult males were present in this population. This was largely unexpected since results from previous removal experiments with blue grouse (Bendell and Elliott 1967; Bendell et al. 1972; Zwickel 1972) produced no evidence for the existence of "surplus" adult males. A reservoir of non-breeding males has been suggested to exist in populations of ruffed grouse (Bonasa umbellus) (Gullion 1967).

Although other removal experiments have been performed on populations of blue grouse (cited above) here is the first substantial evidence that non-breeding adult males exist. If a surplus of non-breeding adults is normally present, why were they not discovered by previous workers?

Zwickel (1972) did not begin removing birds until 17 May. Non-breeding adults may have left the removal area by this time. Also, by this time, testes are regressing (Simard 1964) and a stimulus to initiate territorial behaviour may be low. In all of these earlier studies all, or nearly all, birds were removed from experimental areas. The absence of other birds, both male and female, may have deterred non-breeding males from settling. The potential importance of the presence of other males is suggested by results obtained by McNicholl (1978) who found that male blue grouse tend to hoot in groups. Since previous experiments involved total removals, but mine only selected removals, perhaps the difference in experimental design accounts for the difference in results. In addition, the population used by Bendell et al. (1972) was declining and all adult males there may have been obtaining preferred sites.

Bendell and Elliott (1967) concluded that territorial behaviour did not limit the breeding density of blue grouse. However, presence of non-breeding adult males, which are physiologically capable of breeding, suggests that territorial behaviour can limit the density of breeding males. Klomp (1972) indicated that territorial behaviour could not limit numbers unless all suitable space was occupied. How should unoccupied transient sites be considered then? Since some males apparently delay breeding because persistent sites are not secured, perhaps only optimal areas should be considered. In any event territorial

behaviour cannot be ruled out as a factor influencing the density of breeding male blue grouse.

Why might non-breeding adults not select transient sites for territories since some are always vacant? Nonterritorial adults may behave like yearlings. Even as two year olds some may be unable to secure persistent sites. Rather than occupying transient sites, to which they would be committed in future years, it may be advantageous to delay breeding and attempt to obtain a persistent site at a later time. As with yearlings, the selective value of delaying breeding will depend on life-expectancy and potential for increased reproduction later (Wiley 1974a, b). We know that survival is higher on persistent sites and that males occupying these areas had more females near them in early spring than those occupying transient sites (Lewis 1979). We do not know, however, whether females preferentially select males on persistent sites to breed with, but if so, selection would be strong for males to delay breeding (Wittenberger 1978) if such a site is not available. Any advantage in not breeding would have to be balanced against the probability of death amongst non-breeders and against the probability of securing a persistent site at a later date.

Brown (1969), in describing density levels, hypothesized that non-breeders should not be present in populations until all optimal and suboptimal habitats are filled. If transient sites are considered suboptimal

habitat, then non-breeding males were appearing before all suboptimal areas were occupied. The behaviour of males could explain why blue grouse failed to comply with Brown's hypothesis. Rather than taking territories in suboptimal areas, non-breeding males may delay breeding so that attempts can be made at securing persistent sites later.

Since testes of replacement males were smaller than those of resident males, an alternative that should be considered is that non-breeders do not occupy territories because they are not sufficiently stimulated to defend them. This does not seem plausible though because even with smaller testes they took territories when persistent sites became available. Perhaps males may not become fully stimulated sexually until territories are occupied, a situation similar to that suggested for female blue grouse by Hannon (1978).

Several questions remain to be answered. How long will males delay breeding before selecting transient sites if persistent sites are not available? How successful are non-breeding adults at securing persistent sites at later times? How does the mortality rate of non-breeders compare with that of residents? As well, the critical question of whether or not males on persistent sites breed more than those on transient sites needs to be examined more closely. Long term radio-telemetry studies may help to answer some of these questions and the availability of reliable solar-powered transmitters now makes this feasible.

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L. G. Sopuck and M. Sullivan provided field assistance and along with W. G. Evans, S. J. Hannon, J. O. Murie, and F. C. Zwickel provided useful comments and suggestions. D. O'Connell and F. C. Zwickel performed most of the necropsies. The study was conducted on lands of Crown Zellerbach of Canada Limited and the cooperation given by them is greatly appreciated. Financial assistance came from the British Columbia Fish and Wildlife Branch, the National Research Council of Canada, and the University of Alberta.

Table 1: Cumulative number of original occupants removed from persistent and transient sites on Comox Burn in 1978.

	April										
Date	11	12	13	14	15	16	17	18	19	20	25
No. of birds removed from persistent sites	2	3	5	5	6	10	10	10	10	11	11
No. of birds removed from transient sites	1	2	5	6	7	8	8	9	9	10	11

Table 2: Number of r
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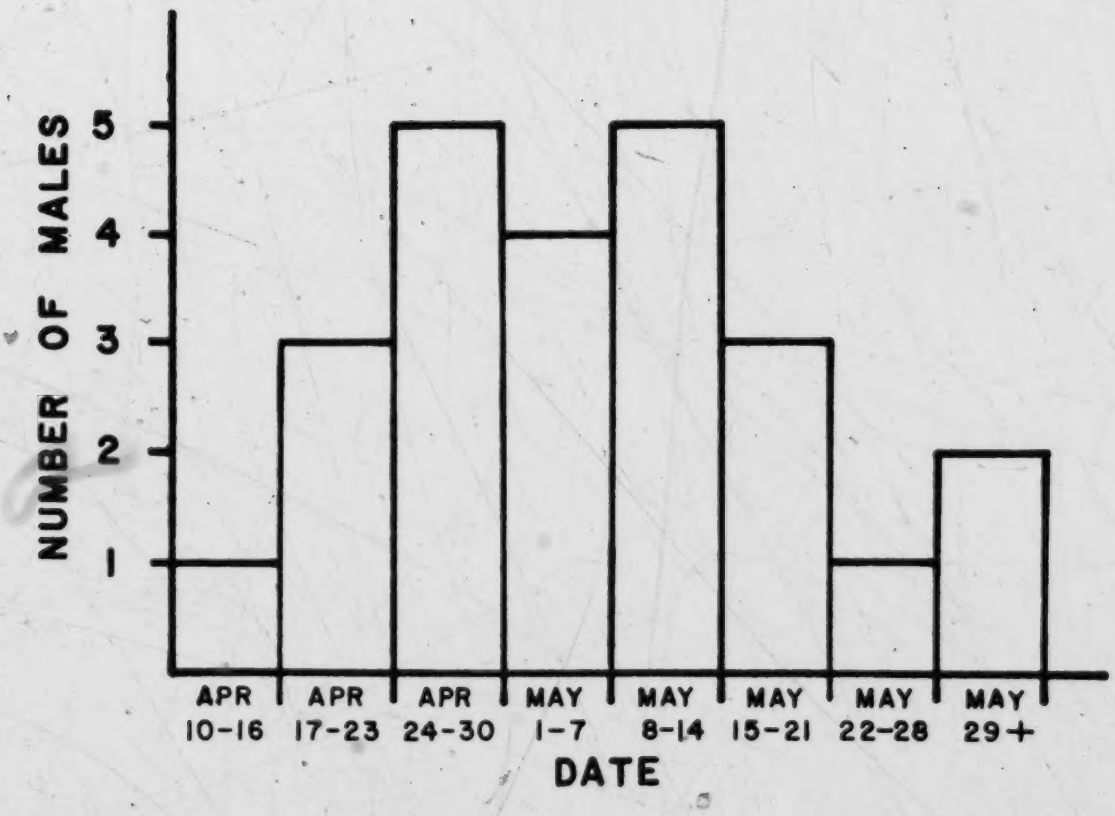

Figure 2: Number of replacement males removed from experimental sites per week, April 10 to week of 29 May.

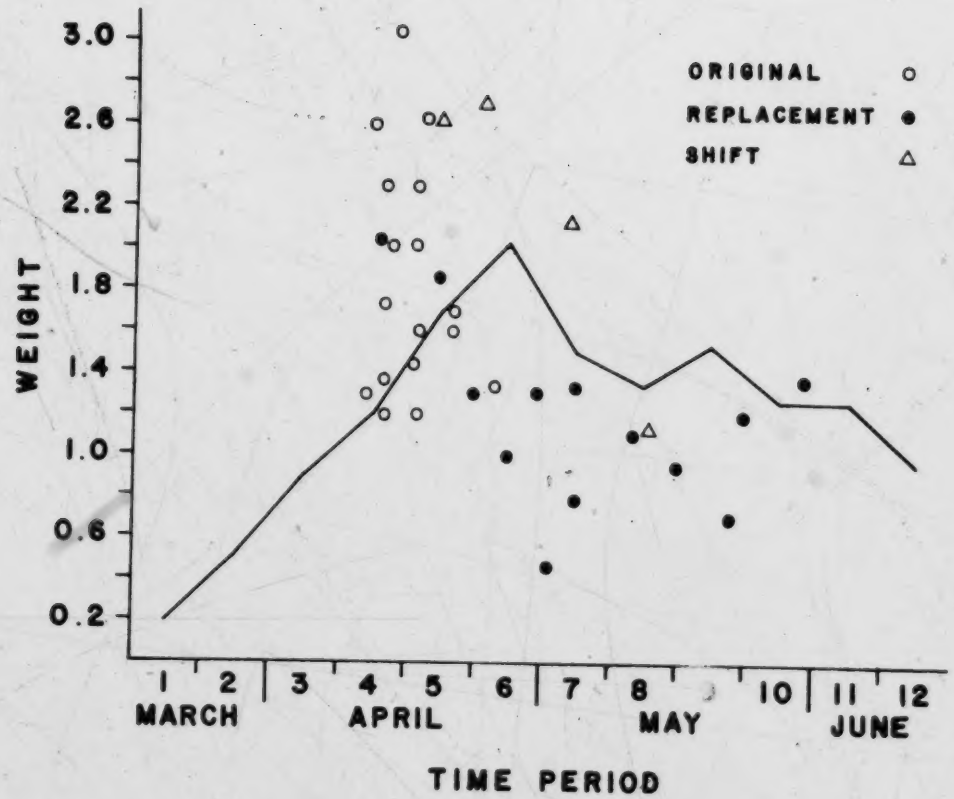

Figure 3: Weights of testes of original occupants and replacement adult male blue grouse on Comox Burn in 1978 as compared to mean weights reported by Simard (1964) for resident territorial males at Middle Quinsam Lake, Vancouver Island (shift refers to males that moved from adjacent nonremoval sites to removal sites).

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Paper 3: CHARACTERISTICS OF PERSISTENT AND TRANSIENT TERRITORIAL SITES OF MALE BLUE GROUSE

Abstract

Vegetative and topographic features of territorial sites of blue grouse (*Dendragapus obscurus fuliginosus*) that were occupied continuously over a ten year period were compared to those of sites used in some years only. Vegetative parameters measured included per cent of ground covered by each species of plant, combined ground level coverage of herbs, shrubs, and trees, and heights and stem densities of trees. Slope of the area around the activity centers of territories and distances from activity centers to nearest areas of equivalent elevation were the topographic characteristics measured. No significant differences were found between these two types of sites with respect to any of these features. Distance to nearest area of equivalent elevation was the only parameter that approached sigrificance. Effects of these structural characteristics of territories on the survival and reproductive potential of the males occupying them are discussed.

Introduction

Male blue grouse are promiscuous (Bendell and Elliott 1967; Wiley 1974) and occupy territories which are primarily used as areas where they can display to and mate with females without interference from other males (Bendell and Elliott 1967; McNicholl 1978). Lewis (1979a) found that male blue grouse used some sites for territories every year and others only intermittently. These were termed "persistent" and "transient", respectively. Males that occupied persistent sites lived longer and had more females near their territories in early spring than those using transient sites. Males occupying persistent sites may therefore have more opportunities for breeding than those on transient sites. Experimental evidence suggests that persistent sites are preferred by males (Lewis 1979b). The question then arises: How do these two types of site differ?

The purpose of this study was to examine selected characteristics, vegetative and topographic, of persistent and transient sites to see if they differ. Although availability of food was examined, structural characteristics that are most likely to affect a male's ability to escape predators and attract and display to females were stressed. These included measurements of availability of cover, "openness" of territories, and relative height of territories in relation to surrounding areas. Territories tend to be located on elevated areas that are relatively open (Bendell and Elliott 1966, 1967) and

these features may affect a male's chances of breeding.

F. C. Zwickel and M. Sullivan provided helpful discussion and suggestions and M. Sullivan assisted in the field. Studies were conducted on lands of Crown Zellerbach of Canada Limited and financial support came from the British Columbia Fish and Wildlife Branch, the National Research Council of Canada, and the University of Alberta.

Study Area

Comox Burn, a 485 ha area on the east slope of Vancouver Island, British Columbia, approximately 14 km west of Courtenay, served as the study area. This region is intermediate between the Douglas fir (Pseudotsuga menziesii) and western hemlock (Tsuga heterophylla) biogeoclimatic zones (Krajina 1965).

Comox Burn was logged by clearcutting between 1947 and 1961 and in September 1961 was burned by wildfire. Replanting with Douglas fir was almost complete by 1964. In 1978, when vegetative parameters were measured, vegetative structure of parts of the area were "dense" or "very dense" but the majority was still "open" (see Bendell and Elliott (1967) for classification criteria). Additional information about the study area can be found in Zwickel and Bendell (1967, 1972).

Methods

In spring 1978 a removal experiment was conducted on Comox Burn to examine rates of replacement to persistent and transient sites (Lewis 1979b). The same sites (11 persistent, 11 transient) used in that experiment were utilized for comparison in this study. Since rates of replacement to populations of blue grouse may be reduced in areas with "dense" or "very dense" vegetative structure (Redfield *et al.* 1970), all territorial sites selected for the removal experiment were in areas classified as "open".

Species and per cent ground cover of herbs, shrubs, and trees were measured in August using the canopy coverage method (Daubenmire 1959). Per cent area covered by debris (logs, stumps, etc.) and amount of area represented by bare ground were also recorded. On each territory a point within the activity center (Lewis 1979a) was selected at random. One canopy coverage plot was located at this point. Four additional plots were placed one meter away, one in each of the 4 cardinal compass directions. This gave a total of 55 plots from the activity centers of each type of territorial site (persistent and transient). These data were used to compare vegetative cover of the activity centers of persistent and transient sites. Four more plots on each territory were located in each of the 4 cardinal compass directions, at 20 meters from the central plot within the activity center. These plots plus that in the center were used to evaluate plant coverage on the territory as a whole.

Canopy coverage of food plants within the plots covering the whole territory were used to estimate availability of food.

A technique similar to that outlined by De Vos and Mosby (1971) was used to estimate ground level density of herbs, shrubs, debris, and trees within each teritory. A square board (30.5 x 30.5 cm) with a checkerboard pattern of 8 red and 8 white squares painted on it was used; this board approximated the dimensions of a grouse. Within the activity center of each territory, a tree stump that had been used as a singing post (determined by previous knowledge or presence of faecal droppings) was selected as an observation point. The cover board was placed on, and perpendicular to the ground 5 meters away and in a northerly direction from this point. An observer positioned so as to simulate a grouse standing on the stump then counted the number of squares that were visible. Squares more than half hidden by debris or vegetation were not counted. Seven additional measurements were made by repeatedly moving the board 5 meters in a linear direction away from its previous position while the observer remained in place. This procedure was repeated towards the east, south, and west, giving 32 observations per territory. These measurements were made in early May corresponding to the period of peak breeding on Comox Burn (Zwickel 1977) and were used to give an estimate of visibility and openness within each territory.

Heights and stem densities of trees were estimated on each territory. These estimates give an additional

indication of the openness of a territory. Within each territory a tree was selected by standing in the middle of the activity center and walking in a random direction to the nearest one. The height of and distance to the nearest 10 trees from this central tree were then measured. No distinction was made between species but Douglas fir was by far the most prevalent species. Similar sets of data were recorded from 3 more locations in each territory. The central trees for these additional plots were selected by again standing in the middle of the activity center and walking to the nearest tree using directions at 90, 180, and 270 degrees to the original random direction. Distance from the central tree to the nearest tenth tree was used as an index of stem density on a territory.

Slopes around the activity center were estimated in 4 directions on each territory by measuring the incline of a string stretched between 2 poles set perpendicular to the ground and 10 meters apart. The initial slope was taken in the direction of the general exposure of the area, beginning at the middle of the activity center. The remaining 3 were in directions 90, 180, and 270 degrees to this. Uphill slopes were assigned a negative value. The total of these 4 measurements was used as an estimate of the average slope around the activity center of each territory.

Aerial photographs viewed stereoscopically were used to estimate distances from activity centers to nearest areas of equivalent elevation. This measurement gives an indication

of the relative height of the territory in relation to the surrounding area. If a territory was situated on a hillside and had no distinct height of land associated with it this distance was recorded as 0.

Subjective ratings of openness of overstory and understory were made independently by 2 people. Ratings were based on a scale of 1 to 10, with lower values representing greater openness. In general, ratings of openness of overstory represented evaluations of coverage produced by trees while openness of understory corresponded to visual estimates of coverage of herbs, shrubs, and debris at ground level.

Statistical comparisons were made with t-tests unless otherwise noted and probability levels of 0.05 or less were accepted as significant.

Results and Discussion

Data gathered from long-term studies of blue grouse suggest that predation on territorial males may be relatively heavy during the breeding season (F. C. Zwickel, pers. comm.). To examine availability of cover on persistent and transient sites, per cent coverage of all potential cover items was grouped into 3 categories; debris, trees and shrubs, and herbs. The first 2 represent cover present year round while herbs are significant as cover only in summer. In all 3 categories activity centers of persistent and transient sites did not differ with respect to amount of cover. This was also true for territories as a whole (Table 1). Tree heights and stem densities were also similar on persistent and transient sites (Table 2). As indicated earlier, males on persistent sites survived longer than those on transient sites. Assuming that predation is a major source of mortality this suggests that persistent sites offered better security from predators than transient sites. Since the two types of sites did not differ in cover measures, perhaps it is the dispersion of cover items, rather than amount, which is important. Alternatively, males on persistent sites may have better vantage points from which to detect predators or they may be more wary than those on transient sites.

The importance of open areas on territories of blue grouse has been noted by several authors (Bendell and Elliott 1966, 1967; Blackford 1958, 1963; Martinka 1972). Open areas increase visibility and allow males to detect the

presence of females and potential predators. In addition, blue grouse have elaborate mating displays (Hjorth 1970; McNicholl 1978; Stirling and Bendell 1970) and open areas may be important for the performance of these activities. Openness of territories was evaluated by using data from 3 sources; amount of bare ground in canopy coverage plots, subjective ratings of openness of overstory and understory, and cover board readings which gave an indication of the density of vegetation and debris at ground level. Again, no differences were found between persistent and transient sites by any of these methods (Table 3). Amount of cover and openness will be inversely related. Both may be important to territorial males, the first with respect to survival, the second to breeding activities.

Male blue grouse signify occupancy of a territory by hooting (singing) and in doing so attempt to attract females (Bendell and Elliott 1967; McNicholl 1978). The distance that this song may travel will be affected by the topography of the territory and surrounding area. Bendell and Elliott (1966, 1967) reported that territories were usually located on elevated areas. This is also true on Comox Burn. Thus, topography may affect the suitability of a site as a territory. Neither average slopes around activity centers nor distance to nearest area of equivalent elevation were different between persistent and transient sites (Tables 4 and 5). The difference between the two types of site with respect to nearest area of equivalent elevation did approach

significance, however, ($p = 0.12$) and if sample size was increased this might be significant.

Relative availability of food on persistent and transient sites was compared by summing per cent cover from canopy coverage plots of major food plants on each territory. Species considered as major food plants were bracken fern (*Pteridium aquilinum*), Douglas fir, hare's ear (*Hypochaeris radicata*), Oregon grape (*Mahonia nervosa*), red huckleberry (*Vaccinium parvifolium*), salal (*Gaultheria shallon*), strawberry (*Fragaria* spp.), trailing blackberry (*Rubus ursinus*), vanilla leaf (*Achlys triphylla*), and willows (*Salix* spp.). Average ground cover of these plants was similar for persistent and transient sites ($p > 0.1$). This technique gives only a gross estimate of food availability and does not take into consideration the fact that some types of food (e.g. berries) are present only during certain periods. Also, per cent ground area is not necessarily a good estimate of the volume of food provided by each species. However, in spring, when territorial and breeding activities are greatest, males are subsisting on a diet consisting mainly of conifer needles (King 1968). Intuitively, it seems unlikely that food in this form could be limiting since the entire area is comprised of Douglas fir plantations. Nevertheless, quality of food could be critical (Moss *et al*. 1975; Watson and Moss 1972). The importance of this factor on selection of territorial sites is unknown but other studies suggest that densities of blue

grouse are not related to the nutrient quality of the soil or the nitrogen content of the vegetation (Zwickel and Bendell 1972), and the density of territorial males remained the same on one study area after fertilization with urea (Zwickel et al. 1979).

Thus, persistent and transient sites did not differ with respect to any of the variables measured. Also, no significant difference was found when all parameters were combined and compared in a single multi-variate test (Hotelling's $T^2 = 26.95$, $p > 0.05$, Morrison 1967).

Martinka (1972), working with blue grouse in Montana, compared vegetative and topographic features of territories used continuously and intermittently over an 8 year period. He also found no differences between these two types of site with the exception that those with continuous occupancy by the same male were located at higher elevations. Elevation per se may not be important, but rather the height of the territory in relation to the surrounding area, as suggested by my data.

Comox Burn has changed from an area nearly barren of vegetation following the wildfire of 1961 (Zwickel and Bendell 1967, 1972) to one with vegetative structures ranging from "very open" to "very dense". Vegetative structures on territorial sites have therefore undergone dramatic changes. Some persistent sites on Comox Burn had very little vegetation in 1969 but by 1978 they were "very dense" (Lewis 1979a). Despite these changes in vegetative

structure, recruitment to these sites was not affected. Thus, it is not surprising that persistent and transient sites did not differ markedly with regard to vegetative variables.

Boag (1976) stressed the importance of social interactions in determining where ruffed grouse (Bonasa umbellus) settle. Territorial sites on Comox Burn tended to be uniformly spaced, however, and transient sites were located randomly with respect to persistent sites (Lewis 1979a). Thus, social interaction did not seem to determine whether a site was used every year or not.

If persistent sites are more suitable for territories than those used intermittently, it remains to be explained why. Although survival and breeding potential appear greater on persistent sites, I found no differences in vegetative and topographic features between them which might affect mortality and mating success. Perhaps behavioural differences exist between males occupying the two types of sites. For example, males on persistent sites may be dominant over neighbouring males and females may prefer to breed with them. McNicholl (1978) has shown that in groups of male blue grouse that sing together, certain males show singing dominance. However, one must still explain why males with certain behavioural characteristics (e.g. dominance) select persistent sites for territories. Alternatively, some males may be behaviourally different because they occupy "better" territories.

As yet then, the question of why some territorial sites are more suitable than others cannot be explained. At present two alternatives seem to exist. Some sites may be more suitable for territories because they have characteristics which enhance the fitness of the males occupying them, or the suitability of a site may merely be a reflection of characteristics of the male occupying it. If the second alternative is true, the pattern of territorial occupancy displayed by blue grouse (i.e. persistent and transient sites) would not be expected since males with characteristics that enhance breeding potential should be successful irrespective of where there territory is located. Since some sites are used every year there must be something different about them which attracts males. The method used for measuring vegetative and topographic features in this study were designed to detect only marked differences. Perhaps differences are more subtle, in which case more precise techniques would be required. Possibly the answer consists of a combination of these two alternatives. More intensive examinations are needed before this question can be answered.

Table 1: Percentage cover on persistent and transient territorial sites on Comox Burn in 1978.

Cover provided by	Persistent Mean*	S.E.	Transient Mean*	S.E.	P**
A. within activity centers only:					
Debris	12.09	2.82	14.27	2.67	0.58
Shrubs and trees	6.59	2.24	7.32	4.08	0.88
Herbs	4.68	1.92	7.23	3.52	0.54
B. over territory as a whole:					
Debris	19.09	3.77	18.91	2.91	0.97
Shrubs and trees	13.32	2.84	20.73	3.29	0.10
Herbs	7.09	1.57	10.59	3.73	0.40

* Average per cent ground area covered (11 persistent, 11 transient sites).

** Probability level

Table 2: Height of trees (m) and stem density on persistent and transient territorial sites on Comox Burn in 1978.

	Persistent sites		Transient sites		
	Mean	S.E.	Mean	S.E.	P*
Tree height	3.26	0.25	3.15	0.21	0.73
Index of stem density**	4.01	0.19	4.07	0.15	0.84

* Probability level.

** See metnods.

Table 3: Estimates of openness on persistent and transient territorial sites on Comox Burn in 1978 (see text).

	Persistent sites		Transient sites		
	Mean	S.E.	Mean	S.E.	P*
Amount of bare ground**	53.68	6.82	44.50	7.42	0.37
Cover board index	73.36	15.37	56.18	9.00	0.35
Subjective index***					
-overstory	5.09	0.53	5.23	0.37	0.83
-understory	3.77	0.45	4.32	0.42	0.38

* Probability level.

** Per cent bare ground within activity centers (canopy coverage method).

*** Average of visual estimates by 2 observers based on a scale of 1 to 10, 1 = least cover, 10 = greatest.

Table 4: Average slope (degrees) of activity centers of persistent and transient territorial sites on Comox Burn.

	Persistent sites		Transient sites		
	Mean	S.E.	Mean	S.E.	P*
Slope	36.73	6.47	28.64	8.53	0.46

* Probability level.

Table 5: Mean distances (m) from activity centers of persistent and transient territorial sites on Comox Burn to nearest area of equivalent elevation.

	Persistent sites		Transient sites		
	Mean	S.E.	Mean	S.E.	p*
Distance	143.27	46.08	60.36	18.29	0.12

* Probability level.

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CONCLUDING DISCUSSION

The question of how numbers of animals are regulated is a problem that intrigues many ecologists. Several theories, each invoking different mechanisms, have been proposed to answer this problem. In general, these can be grouped into two schools of thought. In the first, factors outside, or "extrinsic" to the animals, such as constraints of weather or availability of food, are considered critical (e.g. Andrewartha and Birch 1954; Lack 1954, 1966). Proponents of the second school believe that populations are self-regulated by "intrinsic" mechanisms involving such things as social behaviour, genetics, and physiology (e.g. Chitty 1967; Christian and Davis 1964; Krebs 1978; Wynne-Edwards 1962). Here, numbers of animals are considered to be regulated by mechanisms that may or may not be related to some extrinsic factor (see Clark et al. (1967) for a general review).

Population studies of blue grouse on Vancouver Island have been designed to examine the importance of several of these proposed factors and/or mechanisms in regulating breeding densities in this species (Bendell 1955; Bendell and Elliott 1967; Redfield 1972; Zwickel and Bendell 1967, 1972; Zwickel et al. 1979). The most recent research has emphasized the study of mechanisms because this might help to elucidate how populations are regulated and help us to understand if regulation is ultimately related to some limiting resource. Results from removal experiments

indicated that surplus yearlings of both sexes were available in spring to inhabit areas artificially depleted of residents (Bendell et al. 1972; Zwickel 1972). These experiments indicated that behavioural interactions in spring immediately prior to breeding limit the number of yearlings that enter breeding populations (Bendell et al. 1972; Zwickel 1972).

Even though adult males are territorial, neither territorial behaviour nor the males themselves have been viewed as important in the regulatory process (Bendell and Elliott 1967; Zwickel 1972). This conclusion seemed valid since all available space was not occupied by territorial males and since all adult males were believed to hold territories. Also, since males are promiscuous, it is difficult to conceive how males might limit breeding without invoking group selection as suggested by Wynne-Edwards (1962) (cited in Selander 1965). However, results from my experiment strongly suggest that some adult males do not occupy territories, hence are non-breeders. Thus, the role of adult males and territorial behaviour in regulating numbers of breeders, at least in males, must be reevaluated.

Territorial behaviour as a mechanism regulating the size of animal populations has received much attention (e.g. Brown 1969; Hinde 1956; Klomp 1972; Stokes 1974; Watson and Moss 1970). It is generally accepted that territorial behaviour limits breeding densities if no resource, such as food or nest sites, is limiting and if some individuals that

are capable of breeding are prevented from doing so by such behaviour. My results suggest that male blue grouse satisfy these criteria. Therefore, males should be considered as potentially important in the regulatory process. Perhaps densities of males and females are regulated separately as suggested for the field vole (Microtus townsendii) (Redfield et al. 1978); Hannon (1978) has postulated a mechanism by which female blue grouse can regulate their own density. If sexes are indeed regulated separately in blue grouse then the question of why sex ratios are equal in this species (Zwickel and Bendell 1967, 1972) is of interest.

The subject of delayed breeding in young individuals often arises in discussions of population regulation and has been a topic of much interest among population biologists (e.g. Selander 1965; Wiley 1974a, b; Wittenberger 1978). One argument is that delayed breeding will evolve if individuals that delay breeding produce more offspring over their lifetime than those that breed at an early age. This can occur if early survival and/or later reproduction are increased by not breeding when young (Wiley 1974b). My results provide evidence that this might be true for yearling male blue grouse. If yearling males selected transient sites for territories their life expectancy, and perhaps annual breeding success, would decline. Whether or not this produces a selection sufficiently strong to result in the evolution of delayed breeding in yearling males remains to be answered. However, since even some adults

apparently delay breeding because persistent sites are not obtained, the evidence is consistent with such a conclusion.

Two major points with regard to population regulation in blue grouse are thus apparent from my studies. First, in contrast to previous hypotheses, adult males may play a role in determining the size of breeding populations and second, support for Wiley's (1974a, b) explanation for non-breeding in yearling males is produced. Arguments supporting these proposals are based on the assumptions that persistent sites are more suitable than transient sites for territories and that breeding success is enhanced by occupation of a persistent site. My data strongly support the first assumption, and less directly the second.

If persistent sites are more suitable for territories than transient sites then there should be demonstrable differences between them. However, these two types of site did not differ with respect to any of the vegetative or topographic variables I measured. Nevertheless, since survival of the two groups of males occupying these sites differed, I believe the sites must differ in some way. The alternative, that the observed demographic differences are due to the behaviours of the males seems unlikely since males showed a preference for persistent sites. Perhaps more intensive studies of the features of the two types of site would reveal differences between them.

My results provide a stimulus for further research since some critical questions still remain. Perhaps the most

pressing need is to test the hypothesis that breeding success is greater in males that occupy persistent sites than those using transient sites. This hypothesis may be difficult to test, however, since copulations are almost never witnessed in the field and females do not remain with the male with which they breed (Bendell and Elliott 1967). A second question is: Why do some adults select transient sites for territories while others apparently delay breeding until 3 to 5 years of age if persistent sites are not obtained? The answer to this question is undoubtedly complex and probably includes such factors as individual variation in habitat preference, individual differences in behaviour, and perhaps chance. Finally, factors that may affect a male's chances of obtaining a persistent site need to be determined and more intensive examinations of structural features of persistent and transient sites are recommended.

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